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**Evaluation of Balance between Fishes and Available Fish
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Evaluation of Balance between Fishes and Available Fish Foods in Multispecies Fish Culture Ponds in Taiwan

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ABSTRACT

Evaluation of the condition of balance between fishes and available fish foods in impoundments of multispecies fish culture in Taiwan was made by analyzing the quantitative interrelations between the standing crop of fish-food biota and the stocked fishes of ecologically different species in a 6-hectare pond with organic fertilization and feeding, and 99 irrigation reservoirs with a total water surface area of 697 hectares. In a balanced condition, the growth rate of plankton, macrophytes, benthos and nekton (exclusive of stocked fishes) kept pace with the rate of consumption by the fishes, respectively, of planktophagic, macrophytophagic, benthophagic, and nektophagic species within the impoundment. Studies of the interaction between the fishes and the fish-food biota in the two types of impoundments of multispecies fish culture with different management methods shed considerable light on fish food utilization and competition in pond ecosystems. On the principle of fish production, these studies provide a basis for improved management of impoundments.

INTRODUCTION

Association of fish species of different food habits for effective use of available fish foods in the pond is one of the most important management techniques for maximum fish production. This idea of multispecies fish culture was derived originally from the Chinese philosophy of harmony, i.e., harmonization of the relations among man, matter, and nature. Chinese fish farmers, by generations of experience, have so managed their ponds that the fish they stock harmonize with available fish foods and among fish species within the pond. This balanced condition between fishes and available fish foods is the principle of the Chinese system of pond management.

Multispecies fish culture is the synonym of polyculture in Europe-U.S.S.R., and mixed fish culture in the Mediterranean area (Yoshou, 1966), but implies a different concept to the balanced fish population of warm-water ponds for game fish in the U.S.A. (Swingle, 1950). This system of fish culture has recently received an increasing amount of interest from fish culturists in many parts of the world and three major culturing species of Chinese carps, the silver carp (*Hypophthalmichthys molitrix*), the bighead carp (*Aristichthys nobilis*), and

the grass carp (*Ctenopharyngodon idella*), have widely been introduced into many countries in Asia, Africa, Europe, and North and Central America (Nair, 1968). In emphasizing this system of fish culture to be an approach to increase pond productivity, Yoshou (1966) stated that the goal of rational pond management is to utilize the existing ecological niches in the pond to produce fish to its carrying capacity; fertilization and feeding enrich the food niches, but only a properly associate fish population of ecologically different species will efficiently utilize the enriched food niches to attain the carrying capacity of fish production. Results obtained from experiments on stock manipulation of fish populations in ponds at Auburn (Swingle, 1966), indicate that while the highest fish production of a single species was obtained by raising a plankton-feeding fish, highest total fish production per unit area could only be obtained by using a combination of species of different food habits. Swingle also stated that one of the most important problems in fish culture is to determine just what combination of species is the most effective in utilizing available fish foods. Multispecies culture of carps in China and India has been practiced for many centuries, yet no biologically-sound measures have been developed to determine the balance between the stocked fishes and the available fish foods, or the correct rate of stocking to obtain the fish productive capacity. This

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stems from lack of basic research on the interaction between fish populations and available fish-food biota in ponds.

This paper deals with ecological measures in evaluating the condition of balance between the standing crop of biotic constituents and the stocked fishes with different food habits in the impoundments of different environments and different methods of management.

DESCRIPTION OF THE IMPOUNDMENTS AND THEIR MANAGEMENT PRACTICES

Tainan fishpond is a 6.0-hectare pond located in southwest Taiwan. It was constructed in alluvial soils with sandy loam in the surface soil and is supplied by underground discharges of water. Pond water levels fluctuate with the seasons, ranging from 0.5 to 1.0 m deep during the February to May dry period and 2.0 to 3.0 m during the rest of the year. The water is chemically hard, with pH values of 8.4 to 8.8 occurring just before daybreak. Surface water temperature ranges from 9 to 32 C throughout the year. Temperatures below 20 C occur only between December and March.

This pond has been managed by experienced fish farmers for centuries. Management practices, including stocking, fertilization, and supplemental feeding, were developed by fish farmers of past generations and these methods have been used for many years without modification. Fingerlings of various species, 3 to 9 cm in total length, are stocked in the pond in February–March, except that piscivorous species are stocked after April. Fish are harvested the following December–January by draining the pond. Various kinds and amounts of organic materials are added between May and December when the water level of the pond is high. Organic materials, such as rice bran, are usually applied late in the rearing season when the fish population is dense, and are also used at other times during the rainy season when natural fish-foods appear insufficient for fish growth.

The Taoyuan reservoirs are a part of the Tachun Irrigation System which includes a series of 241 reservoirs with a total water surface area of 2,112 hectares. These reservoirs are located in northwest Taiwan; 99 of these reservoirs with a total water surface area

of 697 hectares were selected for fish culture. Size of individual reservoirs ranged from 3.5 to 22.0 hectares. Surface soils in this region appear reddish-brown and are clay loam to light clay in texture. Water level is maintained by a series of canals connected upstream with the River Tamshui. Reservoir water levels fluctuate with the irrigation of ricelands and range from 0.5 to 4.0 m in depth. The water of these reservoirs is chemically soft, with pH values of 6.0–7.8 occurring just before daybreak. Annual temperature range of the upper layer of water varies from 7 to 31 C. Temperatures below 20 C occur between November and April.

Use of these reservoirs for fish culture began in 1957. The fish stocking procedure was similar to that developed in the Tainan fishpond, with slight modifications in accordance with the specific fish-food organisms produced in individual reservoirs. A great majority of these reservoirs received no manures or supplemental feeds because of frequent water outflow. Fish were harvested from November to January, the fallow period in rice culture. These reservoirs were managed by a group of retired army veterans who maintained accurate records of all operations, including the weights of various species of fishes harvested.

METHODS

Quantitative Determination of Plankton

A total of 42 sets of water samples was obtained from August to November at bi-weekly intervals in 1952, and at weekly intervals in 1955 and 1956 for Tainan fishpond. Sampling was made by a Kemmerer water sampler. Taoyuan irrigation reservoirs were sampled at bi-weekly intervals in September, and occasionally in early October, for three years, 1958–1960. Each set of water samples was taken from 3 to 9 different stations and at 3 depths, namely, upper, middle, and lower water layer in individual impoundments. Plankton organisms were separated from the water samples with a Foerst centrifuge at 15,000 rpm. This method retained not only the plankton but also various forms of organic and inorganic detritus. Dry organic weights were obtained by loss in weight of the dried

TABLE 1.—Species of stocked fishes classified into six groups based on their characteristic food habits

Food habits	Species of fish
Planktophagic	Silver carp, <i>Hypophthalmichthys molitrix</i> ¹
Detritophagic	Grey mullet, <i>Mugil cephalus</i> ²
Zooplanktophagic	Bighead carp, <i>Aristichthys nobilis</i>
Macrophytophagic	Grass carp, <i>Ctenopharyngodon idella</i>
Benthophagic	Common carp, <i>Cyprinus carpio</i>
	Black carp, <i>Mylopharyngodon piceus</i>
Nektophagic	Sea perch, <i>Lateolabrax japonicus</i>

¹ This species feeds principally upon plankton from the water column, and the plankton was composed of 93% microscopic algae, therefore it is also called a phytoplanktophagic species.

² This species feeds principally upon phytoplankton-produced detritus on the pond bottom and it is also called a detritus-phytoplanktophagic species.

materials following incineration. For convenience in evaluating the relationships of plankton and other plants and animals, wet weight of the plankton was used. Weight of standing crop of plankton, in kilograms per hectare, given in this paper was obtained by multiplying the quantity of dry organic matter per unit water volume of the sample by 10, and then by the total volume of the impoundment at the moment of sampling. It was assumed that water content of aquatic organisms approximates 90% of their weight on an ash-free basis. This method of quantitative plankton determination was adopted from that developed by Juday (1926). Quantitative zooplankton determinations were made by filtering water samples through 20-mesh silk bolting cloth.

Quantities of Benthos, Macrophytes, and Nekton

Benthos was sampled with an Ekman dredge. Sampling occurred simultaneously with that for plankton and was made at different areas and depths within the pond and irrigation reservoirs. Quantitative data of the standing crop of the benthos for the Tainan pond were obtained by averaging 378 samples, equivalent to 63 samples per hectare of water surface area. For the Taoyuan irrigation reservoirs, there were 216 samples, equivalent to 3 samples per 10 hectares of water surface area. Macrophytes were collected manually and the areas where they had grown were determined by actual survey. Sampling occurred annually in September in the pond and in August in the irrigation reservoirs. Nekton, primarily macro-crustaceans and miscellane-

TABLE 2.—Species and numbers of fish ranging 3-9 cm in total length stocked in February-March, and the average¹ percent mortalities of these species during a growing period of 11 months in two types of impoundments

Species	Number stocked per hectare	Percent mortality	
		Average	Range
Tainan Pond			
Silver carp	3,500	14	9-19
Grey mullet	9,000	33	25-42
Bighead carp	500	16	7-25
Grass carp	200	10	5-16
Common carp	10,000	39	31-48
Sea perch	300	23	17-30
Total	23,500		
Taoyuan Irrigation Reservoirs			
Silver carp	400	20	16-25
Grey mullet	200	71	60-82
Bighead carp	15	26	16-35
Grass carp	80	20	15-25
Black carp	10	50	40-60
Common carp	200	60	40-80
Sea perch	50	75	50-100
Total	955		

¹ Data are means from a three-year investigation period.

ous small fishes that had not been stocked, was determined by draining the impoundments at the end of the fish rearing season.

Fish Stocking

Stocked fishes were ecologically classified into six groups (Table 1). This method of grouping was based on the characteristic food habits of the fishes, a detailed account of which is given by CFFCESC (1961), and Hora and Pillay (1962). Change of food habits with fluctuations in abundance of preferred foods and size of the fish was at a minimum because: (1) with intensive food competition between species and groups of species of fish, there was little biotic vacancy or vacant feeding niches in the ecosystem, thus reducing facultative feeding; and (2) sizes of stocked fishes were such that there was little change in their food habits within the impoundments. Average numbers of fish fingerlings of various species stocked in the pond and the irrigation reservoirs, and the percentages of their mortalities during the years of investigation are given in Table 2.

Pond Manuring

Kinds and amounts of organic materials used for manuring the Tainan pond in the fish rearing seasons of 1952 and 1955-1956

TABLE 3.—Kinds and dry weights of organic materials used per hectare to manure the Tainan Fishpond¹ annually

Material ²	Amount (Kilograms per hectare per annum)			
	Total dry matter	Fertilizing constituents		
		Nitrogen	Phosphorus	Potassium
Rice bran	1,700	34	33	20
Chicken manure	1,300	19	13	8
Pig manure	1,200	14	6	5
Night soil ³	8,400	200	144	120
	12,600	267	196	153

¹ An average from the years 1952, 1955, and 1956.

² The average moisture contents of rice bran, chicken manure, pig manure, and night soil were, respectively, 13, 17, 20, and 78%.

³ Disinfected by fermentation in sealed tanks before use.

are given in Table 3. In general, there are three paths through which these materials enter the biotic communities: (1) they are directly utilized as food by forage and omnivorous fishes, and possibly other animals such as crustaceans and insect larvae; (2) they are attacked by a variety of micro-organisms, including bacteria, fungi, protozoa, and so forth which are, in turn, consumed by zooplankters; and (3) they release, as a result of the activities of micro-organisms, nutritive substances such as carbon, nitrogen, and phosphorus in forms available to chlorophyll-bearing plants. Consequently, function of these organic materials in food cycles of a pond is similar to that of dead phytoplankton.

CONDITION OF BALANCE

Data of average wet weight of the standing crop of biotic constituents investigated between August–November, and average fish production from populations composed of species with various food habits for 11 months from February–March to the following December–January in the pond and the irrigation reservoirs are given in Tables 4 and 5, respectively.

Since accuracy of the relationships between fishes and available fish-food organisms depends, to a large extent, upon the accuracy of grouping the fishes as to food habits, analyses of contents of fish stomachs were made from time to time, indicating that food items contained in the digestive tracts of the benthophagic fish included a amount of organic detritus produced from higher plants;

on the other hand, insect larvae were often found in the stomachs of macrophytophagic fish. However, the quantitative values of these shifted food items, i.e., the bottom fauna were eaten by macrophytophagic fish, and the higher aquatic plants by benthophagic species, were limited, usually, to less than 10%. It should also be noted that planktophagic fish, i.e., silver carp, also consumed zooplankton. The quantitative value of the latter food item, however, was less than 7.0% that of the total plankton organisms. Therefore, this ecological classification of the fish species appears accurate enough for practical purposes, as the error is less than 10%.

Definition and Symbols

Ecological measures in evaluating the condition of balance between fishes and available fish foods in multispecies fish culture impoundments are made by quantitative analyses of the weight interrelations and weight percentage interrelations between the standing crop of fish-food biota consisting of plankton, macrophytes, benthos, and nekton, and the stocked fishes of ecologically selected species composed of planktophagic, macrophytophagic, benthophagic, and nektophagic forms. The ecosystem of an impoundment in which the growth rate of various groups of fish-food biota keeps pace with the rate of consumption by respective fish groups of different food habits is defined as the fish populations balance with the standing crop of fish-food biota within that impoundment.

Symbols used to indicate various factors studied in the relationships between fishes and groups of fish-food biota within the aquatic environments are as follows: W = weight per hectare, E = percent of total weight of biota (B) or total weight of fishes (F) due to each component group, B = total groups of fish-food biota, and F = total groups of fishes stocked and harvested. The groups within the biota (B) and the groups of fishes feeding upon these groups of biota are differentiated by the following numbers: 1 = plankton, 2 = macrophytes, 3 = benthos, and 4 = nekton excluding the fishes (F) that were stocked. Thus W_{n_1} indicates the weight of plankton and W_{F_1} the weight of planktophagic fish per hectare of pond or irrigation reservoir.

TABLE 4.—Wet weight and E_B values of the standing crops of the biotic constituents in two types of impoundments

	Tainan Fishpond								Taoyuan Irrigation Reservoirs							
	Wet weight in kilograms per hectare				E_B values ¹				Wet weight in kilograms per hectare				E_B values ¹			
	1952	1955	1956	Mean	1952	1955	1956	Mean	1958	1959	1960	Mean	1958	1959	1960	Mean
Phytoplankton	6,353	7,084	6,878	6,772	86.4	89.6	84.5	86.4	522	829	582	654	50.6	63.5	49.6	54.6
Zooplankton	422	486	567	492	5.8	6.2	7.0	6.3	41	47	55	48	3.8	3.6	4.7	4.0
Macrophytes	128	73	150	117	1.7	0.9	1.8	1.5	406	358	367	377	37.2	27.4	31.3	32.0
Benthos	313	213	459	362	4.4	2.7	5.7	4.7	62	65	104	77	5.7	5.0	8.9	6.5
Nekton ²	128	49	83	86	1.7	0.6	1.0	1.1	30	7	65	34	2.7	0.5	5.5	2.9
Total biota	7,344	7,905	8,137	7,829	100.0	100.0	100.0	100.0	1,091	1,306	1,173	1,190	100.0	100.0	100.0	100.0
Total plankton	6,775	7,570	7,445	7,264	92.2	95.8	91.5	92.7	593	876	637	702	54.4	67.1	54.3	58.6
Total plants	6,481	7,157	7,028	6,889	88.2	90.5	87.6	87.9	958	1,187	949	1,031	87.8	90.9	80.9	86.6
Total animals	863	748	1,109	940	11.8	9.5	12.4	12.1	133	119	224	159	12.2	9.1	19.1	13.4

¹ E_B value = the weight percentage of total biota due to a particular biotic group.² Excluding the fish species stocked, but including small wild fishes and crustaceans.

TABLE 5.—Species composition of the fish populations at harvest classified into groups of different food habits in two types of impoundments

	Tainan Fishpond								Taoyuan Irrigation Reservoirs							
	Live weight of fish in kilograms per hectare				E_F values ¹				Live weight of fish in kilograms per hectare				E_F values ¹			
	1952	1955	1956	Mean	1952	1955	1956	Mean	1958	1959	1960	Mean	1958	1959	1960	Mean
Silver carp	2,468	3,044	2,608	2,706	35.8	39.1	36.3	37.1	256	290	240	262	57.8	67.2	60.5	61.8
Bighead carp	896	659	653	736	13.0	8.4	9.1	10.1	25	28	22	25	5.5	6.5	5.6	5.9
Grass carp	207	298	287	263	3.0	3.8	4.0	3.6	110	51	58	73	25.0	12.0	14.6	17.2
Grey mullet	2,461	2,658	2,386	2,502	35.7	34.2	33.2	34.4	7	25	18	17	1.6	5.8	4.7	4.0
Common carp	751	958	1,020	910	10.9	12.3	14.2	12.5	27	24	33	28	6.1	5.6	8.2	6.6
Black carp									5	5	8	6	1.1	1.1	1.9	1.4
Sea perch	110	171	230	170	1.6	2.2	3.2	2.3	13	8	18	13	2.9	1.8	4.5	3.1
Total fish species	6,893	7,786	7,184	7,287	100.0	100.0	100.0	100.0	443	431	397	424	100.0	100.0	100.0	100.0
Planktophagic (silver carp, bighead carp, and grey mullet)	5,825	6,361	5,647	5,944	84.5	81.7	78.6	81.6	288	343	280	304	64.9	79.5	70.8	71.7
Macrophytophagic (grass carp)	207	298	287	263	3.0	3.8	4.0	3.6	110	51	58	73	25.0	12.0	14.6	17.2
Benthophagic (common and black carps)	751	958	1,020	910	10.9	12.3	14.2	12.5	32	29	41	34	7.2	6.7	10.1	8.0
Nektophagic (sea perch)	110	171	230	170	1.6	2.2	3.2	2.3	13	8	18	13	2.9	1.8	4.5	3.1
Phytophagic (silver carp, grey mullet, and grass carp)	5,136	5,998	5,282	5,471	74.5	77.1	73.5	75.1	373	367	316	352	84.4	85.0	79.8	83.0
Carnivorous (bighead carp, common carp, black carp, and sea perch)	1,757	1,788	1,902	1,816	25.5	22.9	26.5	24.9	70	64	81	72	15.6	15.0	20.2	17.0

¹ E_F value = the weight percentage of fish population composed of a particular species.

TABLE 6.—Values of $E_F:E_B$ and $W_F:W_B$ ratios¹ in two types of impoundments

Fish-food biota	Utilization by fish species	$E_F:E_B$ ratios ²		$W_F:W_B$ ratios ³	
		Tainan Fishpond	Taoyuan Irrigation Reservoirs	Tainan Fishpond	Taoyuan Irrigation Reservoirs
Plankton	Silver carp, bighead carp, and grey mullet	0.88	1.22	0.81	0.43
Macrophytes	Grass carp	2.40	0.53	2.24	0.19
Benthos	Common carp and black carp	2.67	1.23	2.51	0.44
Nekton	Sea perch	2.00	1.07	1.98	0.38
Total plants	Silver carp, grey mullet, and grass carp	0.89	0.97	0.82	0.34
Total animals	Bighead carp, common carp, black carp, and sea perch	1.82	1.26	1.70	0.45
Total biota		1.00	1.00	0.92	0.36

¹ Computed from the means of the standing crops of fish-food biota during the period August–November and the fish yield at harvest for three years.

² $E_F:E_B$ = the ratio of E value of fishes to the E value of the group of biota forming their principal food.

³ $W_F:W_B$ = kilograms of the component groups of fish at harvest per kilogram in the standing crop of their principal groups of fish-food biota upon which they feed.

Weight Ratios

Ratios of $W_F:W_B$ for various groups of fish-food biota are given in Table 6. The $W_F:W_B$ is interpreted as the kilograms of planktophagic species in the total fish crop that were maintained, at a minimum, by each one kilogram of plankton in the total biota during a given growing period in the impoundment. The ratio value for $W_F:W_B$ in the irrigation reservoirs was 0.36 which means that, under the system of multispecies fish culture in these irrigation reservoirs in Taiwan, for each one kilogram of fish-food biota in the standing crop, an average of approximately 0.36 kilogram of fishes was able to maintain at the end of a growing period of 11 months.

The principle of carrying capacity of fish production from a mixed fish culture pond, as interpreted by Yoshou (1959), is that the "grand total" capacity of the pond to produce fish is the sum of production of ecological niches existing in the pond, and production of a species or a group of fish from the ecological

niche in which this species or group of species of fish lives, can be increased through man's intervention, by administration of fertilizers or addition of feeds, and so forth. In the irrigation reservoirs that were stocked with fish fingerlings for a growing period of 11 months, the ratio values were $W_{F_1}:W_{B_1} = 0.43$, $W_{F_2}:W_{B_2} = 0.19$, $W_{F_3}:W_{B_3} = 0.44$, and $W_{F_4}:W_{B_4} = 0.38$; while with an equal growing period in the Tainan pond, the values of the above ratios were respectively 0.81, 2.24, 2.51, and 1.98 (Table 6). Higher values of the above ratios in the pond, based on Yoshou's theory, were apparently due to the enrichment of ecological niches in the pond by applying organic matter as fertilizer and feed at an annual rate of 12,600 kg dry weight per hectare (Table 3).

While indirect effects of these applications were measured in approximately 558% increase in fish-food biota, the direct effects from fish utilizing rice bran and manures as feeds are included also in the above ratios.

TABLE 7.—Estimate of weights of fish produced by direct utilization of rice bran and manures in Tainan Fishpond

Fish-food biota	Utilized by fish species	Difference in $W_F:W_B$ ratios between the pond and the irrigation reservoirs	Kilograms food biota in pond	Kilograms fish in pond due to direct feeding on organic manures and rice bran ¹
Plankton	Silver carp, bighead carp, and grey mullet	0.38	7,260	2,758
Macrophytes	Grass carp	2.05	120	246
Benthos	Common carp and black carp	2.07	360	745
Nekton	Sea perch	1.60	86	138
Total			7,826	3,887

¹ Conversion value of organic matter = $12,600/(3,887) = 3.2$.

If it is assumed that the $W_F:W_B$ ratios in the irrigation reservoirs are relatively accurate measures of the relationships without feeding, then it is possible to estimate the kilograms of fish produced by direct feeding in the Tainan pond by multiplying the differences in each ratio between pond and irrigation reservoirs by the weight of the group of fish-food biota in the Tainan pond (Table 7). This gives an estimate of 3,887 kg fish produced from direct feeding upon the added organic matter and 3,400 kg fish produced from feeding on fish-food biota. The conversion of organics added (12,600 kg dry weight) to fish produced by direct feeding is thus estimated as 3.2 to 1.

Experiments conducted in concrete tanks at the Tainan Station indicated that planktophagic fishes and omnivores like the carps failed to grow normally when they were fed exclusively with manures. A similar result was also obtained from experiments on feeding of milkfish (*Chanos chanos*) (Tang, 1967). Organic wastes are poor quality feeds and it seems probable that a mixture of manure with natural food organisms is necessary for good growth.

Weight interrelations between the component groups of fish composing the population and their corresponding constituents of food biota in the standing crop, and dynamics of these interrelationships in the two types of impoundments are discussed in the Section "weight percentage ratios."

Weight Percentage Ratios

The ratio $E_{F_1}:E_{B_1}$ gives the percentage of planktophagic species in the total fish crop for each one percent of plankton in the total fish-food biota. If we assume that the standing crop of biota as measured represents a normally distributed population and the nutritive values of various biota are identical in growing respective fish groups of different food habits, then a balance between the component groups of fish composing the population and their corresponding segments of food biota in the standing crops in these impoundments hypothetically would be expected so that:

$$E_{F_1}:E_{B_1} = E_{F_2}:E_{B_2} = E_{F_3}:E_{B_3} = E_{F_4}:E_{B_4} = 1$$

In the irrigation reservoirs, the mean values of the above ratios were respectively 1.22,

0.53, 1.23, and 1.07 (Table 6). Since E values are percentages, the weighted average of these ratio values is 1.0. If the stocked fishes balanced with the standing crop of fish-food biota in these reservoirs, deviations of the values of these ratios from a hypothetical value of 1.0 were principally attributed to the difference of the nutritive values of various biota. The lower ratio value for macrophytes ($E_{F_2}:E_{B_2}$) is, therefore, understandable upon the basis of their lower nutritive value. Conversion of kilograms of napier grass (*Pennisetum purpureum*) to a kilogram of grass carp was 48:1 in experiments at Malacca (Hickling, 1962); while plankton algae (primarily filamentous blue-greens and the diatoms) to milkfish in Taiwan ponds was 13:1 (Tang and Chen, 1966). At first glance this would lead one to expect a much lower ratio value for $E_{F_2}:E_{B_2}$ in the irrigation reservoirs than that obtained above. However, it must be pointed out that "macrophytes" might better be defined as "macrophyte complex" as it includes higher plants and their associated organisms such as filamentous algae, periphyton, and both ambulatory and attached animals. Thus, the macrophyte complex is much more nutritious than macrophytes alone.

Analyses of deviations from the mean ratio values of $E_{F_1}:E_{B_1} = 1.22$, $E_{F_2}:E_{B_2} = 0.53$, $E_{F_3}:E_{B_3} = 1.23$, and $E_{F_4}:E_{B_4} = 1.07$ in the irrigation reservoirs were made and indicated that $E_{F_1}:E_{B_1}$ and $E_{F_2}:E_{B_2}$ were significantly different from 1.0 beyond the 5% level ($P = 0.04$ for $E_{F_1}:E_{B_1}$ and $P = 0.03$ for $E_{F_2}:E_{B_2}$). The E values of the biota for the groups of plankton plus macrophytes and the fishes for planktophagic plus macrophytophagic species were, respectively, 90.6 and 88.9.

Within the Tainan pond that received high organic fertilization and feeding, the above ratios were respectively 0.88, 2.40, 2.65, and 2.09. This indicated that proportionally the grass carp, common carp (*Cyprinus carpio*), and sea perch (*Lateolabrax japonica*) received greater direct benefit from the organic additives than did the planktophagic group. These two species of carps are known as the most efficient pondfish in utilizing artificial feeds (CFFCESC, 1961, and Lin, 1946). The sea perch is carnivorous and the high ratio of 2.09 probably resulted from the fact that the

standing crop of nekton was measured upon draining at harvest in November–January, and this was not a true indicator of the availability of nekton during the earlier parts of the growing season. Typically, nekton abundance and weight should increase to a peak during the spring and early summer and sharply decline to a point where very little remains during the latter portion of the growing period.

Quality of feeds may play an important role in governing the fish-food biota competition in ponds with feeding. When feeds of low nutritive value in great amount were added, as indicated in Tainan ponds, interspecific competition for biota still existed among the fishes of that population, despite the fact that many of these species resorted to direct feeding. This resulted in high efficiency of fish-food biota utilization in the pond as in the irrigation reservoirs. If, however, a feed of high nutritive value is added in appreciable quantity, the intensity of fish-food biota competition would be relaxed and facultative feeding of fishes would occur to a large extent. This fact has been proved, in part, by Stevenson (1966) who conducted experiments on feeding of grass carp with commercial feeds of high quality in ponds at Stuttgart, indicating that grass carp resorted to eating commercial feeds, but little did they utilize the higher aquatic plants. It is, therefore, supposed that increased availability of feeds with high nutritive value conceivably lowers the efficiency of fish-food biota utilization.

Within the Tainan pond, deviations from the mean values of $E_{F_1} : E_{B_1} = 0.88$, $E_{F_2} : E_{B_2} = 2.40$, $E_{F_3} : E_{B_3} = 2.65$, and $E_{F_4} : E_{B_4} = 2.09$, were statistically analyzed and indicated that only $E_{F_1} : E_{B_1}$ was significantly different from 1.0 at the 5% level ($P = 0.05$). The E values of biota and fishes of this category were, respectively, 92.7 and 81.6.

A number of fisheries biologists have investigated the quantitative relationships between fishes and available fish-food organisms in ponds and lakes in North America (Juday, 1942; Ball, 1948; and others). Most of these biologists were primarily interested in the benthos and nekton respective to the benthophagic and nektophagic fishes in the impoundments. These data were excluded from the present discussion because the primary pro-

duction which constitutes the bulk of the standing crop of fish-food biota was completely out of balance with the fishes of planktophagic and macrophytophagic species within those impoundments.

Interrelations between the values of E_F and E_B in the pond and the irrigation reservoirs are shown diagrammatically in Figures 1 and 2. Dynamics of these interrelationships were indicated by interaction of the variations of E values between each component group of fishes and biota. For example, if a fish that has certain food habits is present in quantities insufficient to utilize its available foods, then facultative feeding by other fishes will occur, thus increasing the apparent E_F value for the groups that resort to facultative feeding, and accompanied by a decrease in that for the species that are present in quantities of insufficiency; while E_B value for corresponding constituents of food biota is consequent to vary vis-à-vis. Thus, the fish populations become unbalanced with the available fish-food biota in the impoundment.

The E values of plankton were 92.7 in the pond and 58.6 in the irrigation reservoirs. This component group of biota was composed of approximately 93% (by weight) of phytoplankton (primarily microscopic algae and minute plankton), and 7% zooplankton (mainly micro-crustaceans and rotifers). Plankton occupied two broad ecological niches: (1) the space of the entire body of the pond water (mostly present in live form), and (2) the stratum of the pond bottoms (existing in detritus form). The E values of planktophagic fishes were 81.6 and 71.7, respectively, in the pond and the irrigation reservoirs. They consisted of three species: the silver carp, the bighead carp, and the grey mullet (*Mugil cephalus*). The former two species fed on the plankton, principally from the water columns, with their gill-rakers; whereas, the latter one fed on the plankton-produced detritus from the beds of the pond bottoms (CFFCESC, 1961; Hora and Pillay, 1962). These planktophagic fishes of ecologically different species played vital roles in efficiency of utilizing the bulk of primary production from the pond that received heavy fertilization and feeding. It was demonstrated in the Tainan pond that a proper grazing of the plankton from the

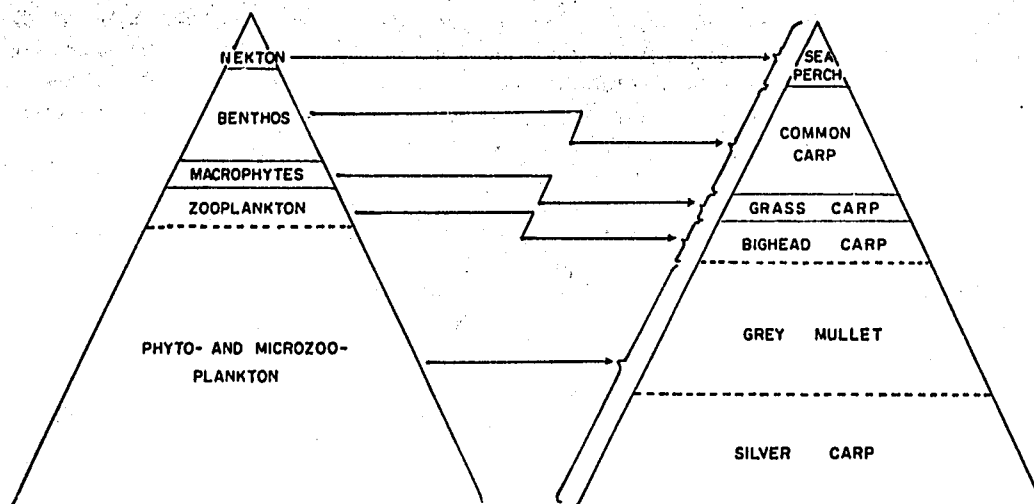


FIGURE 1.—Diagram showing the weight percentage interrelations between the standing crop of fish-food biota and the stocked fishes of ecologically different species in the Tainan Fishpond.

standing crop by planktophagic fishes of adequate quantities could smooth out the abnormal abundance and distribution of phytoplankton, such as *Microcystis* and *Eugleninae* which are the groups of undesirable fish foods (Prowse, 1963). Shallow, heavy growths of these groups of algae often become so dense as to shade sunlight to the lower layers of the water. This forms the so-called "autoshedding" which causes the reduction of primary production and depletion of dissolved oxygen by

reducing the photosynthesis in the lower levels of the water and/or by decaying the surface scums formed by phytoplankton (Swingle, 1947; TFCRI, 1961; and Hopher, 1962). Over-abundance of phytoplankton also causes the unstable food supply to planktophagic fishes as zooplankton would alternate with phytoplankton fluctuation (Swingle, 1947). It has also been demonstrated in the Tainan pond that the presence of intensively-detritophagic species like grey mullet as a component group

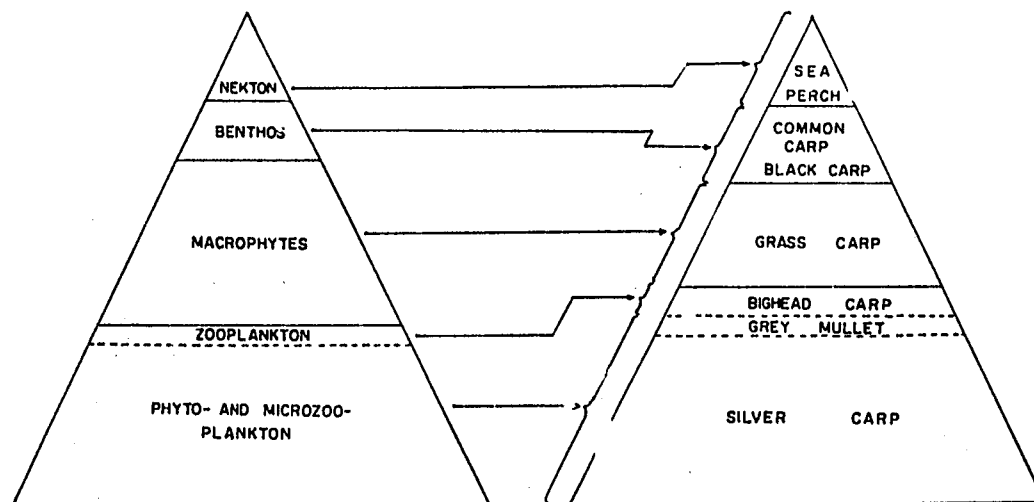


FIGURE 2.—Diagram showing the weight percentage interrelations between the standing crop of fish-food biota and the stocked fishes of ecologically different species in the Taoyuan Irrigation Reservoirs.

of planktophagic fishes, was able to scavenge the stirred bottom sediments produced by the activities of common carp during the process of feeding. Muddy water caused by the presence of common carp is a well-known problem in warm-water pond management (Swingle, 1949). In multispecies fish culture, however, common carp is an indispensable species (CFFCESC, 1961), as its presence, aside from its role in balancing the component biota of benthos, is of benefit to primary production by recycling nutritive substances.

The E values of macrophytes were 1.5 and 32.0, respectively in the pond and the irrigation reservoirs; while those of plankton in the pond and the irrigation reservoirs were 92.7 and 58.6, respectively. The difference of E values between the biota of macrophytes and plankton in the two types of habitats was principally caused by the conflict of environmental requirements for their growth. A detailed account on this was given by Swingle (1947). Correspondingly, E values of planktophagic and macrophytophagic fishes were respectively, 81.6 and 3.6 in the pond; E values in the irrigation reservoirs were 71.7 and 17.2, respectively. These data indicate that grass carp played an important part in balancing the component biota of macrophytes in the impoundments. However, the efficiency of grass carp in utilizing macrophytes depends on the intensity of interspecific competition for food among fishes of a population. In the absence of competition (as shown in the results of experiments conducted by Stevenson, 1966), or in short supply of macrophytes (as the present data indicated in the pond) grass carp feed on other foodstuffs where they are available.

The E values of benthos and nekton were, respectively, 4.7 and 1.1 in the pond; E values in the irrigation reservoirs were 6.5 and 2.9, respectively. Correspondingly, E values of benthophagic and nektophagic fishes in the pond were 12.5 and 2.3, respectively; E values in the irrigation reservoirs were, respectively, 8.0 and 3.1. Apparently the presence of these component groups of fish in a population was necessary to utilize the available source of foods, and, at the same time, they might possibly benefit the yield of the groups of fish that possessed the food habits in conflict with

that of the component biota of benthos and nekton.

It should also be noted that E value for macrophytophagic fish was 13.6 less in the fertilized and fed pond than in the unfertilized irrigation reservoirs; while E values for planktophagic and benthophagic fishes increased 10.0 and 4.5, respectively, under the more fertile condition (Table 5).

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